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IN
ZOOLOGY

Vol. 15, Introduction, pp. i-xxiii June 19, 1916

DEPENDENCE OF MARINE BIOLOGY UPON HYDROGRAPHY AND NECESSITY OF QUANTITATIVE BIOLOGICAL RESEARCH

BY

ELLIS L. MICHAEL

UNIVERSITY OF CALIFORNIA PRESS
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This series contains the contributions from the Department of Zoology, from the Marine Laboratory of the Scripps Institution for Biological Research, at La Jolla, California, and from the California Museum of Vertebrate Zoology in Berkeley.

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1. Introduction

During the past fifteen years the Scripps Institution, and its forerunner the San Diego Marine Biological Association, have been making a biological and hydrographical survey of the waters adjacent to the coast of Southern California. Intensive rather than extensive research in marine biology is the leading idea of this survey, and, although this involves the acquisition of detailed information concerning particular marine organisms, knowledge of the biology of the sea is the ever-present ideal. How is this ideal to be approached? Certainly not by isolated investigations prosecuted under the Institution's auspices by biologists sojourning in Southern California, nor by investigations made for the purpose of advancing any general biological theory. *Continuous and co-ordinative research of several highly trained specialists is the first essential.* Under certain conditions the Institution is

not only glad but eager to give visiting naturalists opportunity for prosecuting their own researches, and special phases of general biology are studied from time to time. It is realized, however, that the ideal sought can be approached only by a programme of research which involves highly specialized and intimately co-ordinated investigations on particular and restricted problems concerning the structure, development, function, behavior, etc., of particular species of marine organisms. But even such specialized investigations can be included in the Institution's marine programme only when subordinated to the larger problem of understanding the sum total of the phenomena of marine plants and animals.

Necessarily, this programme demands thorough investigation of the conditions under which marine organisms live. Knowledge of the environment is as indispensable to a complete understanding of marine organisms as is that of the organisms themselves. "Conditions of the water as to temperature and currents; mineral, gaseous, and albuminoid content, etc., must be known *at the particular time and place to which the biological studies pertain.*" (Ritter, 1905, p. ix.) Chemistry, physics, and hydrography are therefore as indispensable in understanding any marine organism as is morphology, embryology, or physiology. Some biologists, however, hesitate to admit this, not recognizing that their attitude is equivalent to claiming that a marine organism can be completely understood without taking into account its most characteristic quality—its *marineness,* so to speak.

It has been impossible, thus far, for the Institution to conduct chemical investigations on the environment of marine organisms, but much time has been devoted to physical and hydrographical research. Since 1908, when intensive hydrographic research was begun, more than four thousand observations of salinity and density have been made and nearly five thousand surface and subsurface temperatures have been taken within one hundred miles of the coast and between Point Conception (34° 30′ N) on the north and Los Coronados (32° 10′ N) on the south. Within this area two hundred and sixty arbitrarily delimited rectangular "sections," each five minutes on a side, have been investigated, more than five hundred hydrographic observations having been made in some. But this is insufficient. Knowledge of the typical, average, and extreme physical conditions in temperature, density, salinity, and current in each "section," at all depths, at all hours of the day, during each month, and during each of a series of years, is needed to supply an adequate foundation for detailed con-

clusions respecting the relations maintained between marine organisms and the hydrographic elements of their environmental complexes. Such information, greatly restricted because of incompleteness of data, is given by Dr. McEwen in his "Summary and Interpretation of the Hydrographic Observations made by the Scripps Institution," the last paper in this volume.

What justification has the biologist for his deep interest in hydrographic matters? To be sure, they concern the conditions under which marine organisms live, but is such intensive investigation fundamentally valuable and necessary to the biologist? Cannot all essential knowledge concerning the relation between marine organisms and their environments be ascertained as accurately and much more expeditiously by subjecting a few typical organisms to carefully controlled laboratory experiments? Such are some of the questions continually being asked, and the primary purpose of this paper is to inquire into their significance.

The first step in this inquiry consists in distinguishing between *marine biology* and *general biology*. To discuss completely all the implications involved in this distinction would require more space than this paper permits. They have been pointed out over and over again by the Institution's director, to whom I am indebted for many valuable suggestions. The time seems opportune, however, for assembling certain facts revealed by my own research which support these implications and for combining them into an organic whole, to the end that some of the too prevalent misconceptions concerning the nature and function of marine biology may be corrected.

2. Marine Biology vs. General Biology

To understand marine organisms is obviously the function of marine biology. To what extent and why do marine organisms differ in structure, function, and behavior from land and fresh-water organisms, and how did these differences arise? In short, *by virtue of what is a marine organism marine?* This is the central question of marine biology: all others are strictly tributary to it. Possession of gills, swim-bladders, fins, webbed feet, etc., adapts animals, morphologically, to an aquatic but not necessarily to a marine habitat. The fundamental problems of morphology and cytology, regarded as branches of marine biology, are therefore contained in these questions: What are the niceties in structure which adapt marine animals and

plants to a life in the sea rather than to a life on land or in fresh water? How and why did such structural adaptations arise? What is it in structure that prevents marine animals and plants from living on land or in fresh water? Again, the fundamental problems of physiology, regarded as a branch of marine biology, is to determine the niceties in function which adapt marine organisms to a marine life, and to determine how and why such functional adaptations arose. Similarly, the central embryological problem concerned in marine biology is to determine what structural and functional adaptations are involved during successive stages in the life-histories of marine animals and plants, and to determine how and why these adaptations vary. Finally, the purpose of ecology, as a branch of marine biology, is to determine how marine animals and plants are related to every element of their environments, and to determine how they behave so as to maintain these relations.

Yet the belief in many quarters is that, unless the marine biologist devotes his energies toward proving or disproving some evolutional or other widely promulgated theory, his research is devoid of scientific merit. Only last summer a prominent biologist plied me with these questions: What is your study of the relation between chaetognaths and their environments contributing toward an understanding of evolution? What light is it throwing upon the hereditary process? It was clearly implied that, if I could not foresee how it would bear on some dominant theory, my research was superficial and unimportant. But does an animal do nothing important except evolve? Does the meaning and significance of life consist solely in the process by which one individual develops from another? Is it superficial and unimportant to measure the relations between organisms and their environments when *life is wholly dependent upon maintaining these relations?*

The marine biologist is not committed to investigating any phase of evolution or heredity except as it concerns the evolution and heredity of marine organisms, but he is committed, primarily, to finding out what marine organisms are—as such. Incidentally, of course, he will contribute toward a better understanding of the laws of evolution, heredity, variation, and so on, and he will aid in solving many morphological, embryological, and other problems; but only as by-products of his primary obligation—to understand marine organisms.

Broadly interpreted, this conception of marine organisms is that the significance of no phenomenon essential to the life of any marine

organism can be fully understood so long as any other phenomenon likewise essential to it is entirely ignored. This does not imply that the marine biologist must set out with a grim determination to investigate exhaustively, without rhyme or reason, every organism in the sea. Such a course would be folly indeed. But it does predicate that the point of view with which any particular problem is attacked must be so broad and comprehensive as to forestall the too frequent claim that the "ultimate" mystery of life is about to be discovered. It implies that continuous and intimately co-ordinated investigations in morphology, embryology, cytology, physiology, ecology, are required in order that headway may be made toward solving the problems of marine biology. Every problem investigated must be subordinated to this conception; each must be so defined and studied as to contribute its quota toward understanding marine organisms.

Many prominent marine biological institutions, however, regard marine organisms from a quite different point of view. Consider, for example, the Woods Hole Marine Biological Laboratory.[1] No one alive to the progress of American biology during the past three decades can fail to attribute a large part of this progress to the influence of this laboratory. Yet, strictly speaking, scarcely a single investigation carried on under its auspices has been one in *marine* biology, but rather, as Ritter (1905, p. ii) has aptly stated: in "*general biology prosecuted by researches on marine organisms.*" To quote further: "The user of marine organisms in such investigations is quite indifferent to everything concerning them that does not bear directly upon his particular problem. He puts aside the marine animal after it has served his purpose without having even noticed, perhaps, the major part of its traits and qualities and the questions concerning it." Again (p. ii) he says: "The investigator makes use of animals and plants that live in the sea in general biological researches. That these organisms happen to be marine is an incident merely. The investigator turns away from them without hesitation when others, from whatever source, come to hand that suit his purpose better." The investigator with such aims makes no attempt to understand marine organisms as such.

Perhaps the difference in point of view will be more clearly revealed by considering the aims and work of the Naples Zoological Station,

[1] There are in reality two marine biological laboratories at Woods Hole. One is locally known as the "M. B. L." and the other as the Fisheries Station. Noteworthy researches have been prosecuted at both, but these remarks relate primarily to the M. B. L.

the world's most renowned marine laboratory. Here the lines of investigation are distinctly twofold. Like the policy of the Woods Hole Laboratory, that of the Naples Station facilitates research in the widest sense, and no effort is made by the Station to influence the lines of investigation of those who occupy the "research tables." The investigator is permitted to pursue any sort of research he chooses. For example, a morphologist may study the pituitary body, hypophysis, optic chiasma, auditory vesicles, etc., of a particular species of marine fish because he believes that peculiarities in their structure will aid in understanding the origin and evolution of homologous structures in all vertebrates. His investigation, so far as concerns that particular species of fish, is restricted to a dead brain. How and why the peculiarities in structure are correlated in the living fish with other peculiarities in structure, with peculiarities in function, and with peculiarities in behavior, which all together make the fish the particular species of marine fish that it is, are questions which give no direction to his research. In short, his investigation is one in the general morphology of the brain or parts of the brain: a fresh-water fish might serve his purpose equally well. Again, a physiologist may study phosphorescence in *Gonyaulax* because he believes its unique manifestation in this plant will aid in understanding similar phenomena in all phosphorescent organisms. The fact that the uniqueness, which causes him to study the phenomenon in *Gonyaulax* rather than in a fire-fly, is correlated with other unique functions, structures, and behaviors which all together adapt this plant to a marine habitat has no effect on his investigation. His problem is phosphorescence, and the particular organism with which he deals is an incident only. Finally, a cytologist may study chromosomal behavior during spermatogenesis and oögenesis in a chaetognath because he believes that certain oddities in the monoecious nature of the animal may so effect this behavior as to aid in understanding chromosomal behavior generally. Here, again, the fact that the monoecious nature of the animal relates to an animal having structures, functions, and habits typical only of chaetognaths does not influence the investigation. The cytologist is studying the general cytology of germ cells, and the particular organism dealt with is an unavoidable incident. Similarly with respect to most other investigations. Interest is centered in the general theoretical bearing of the structures and functions investigated, and not in the organisms to which they pertain. In so far as the Naples Station has occupied itself with studies of this type it has

been devoted to researches in general biology which only incidentally contribute to marine biology.

But the Naples Station is also engaged in a second enterprise having for its object, as manifested in its magnificent monographic series *Fauna and Flora*, exhaustive knowledge of the fauna and flora of the Gulf of Naples and the Mediterranean Sea. These monographs, it is true, relate mainly, though not entirely, to the structure of the organisms but, in so far as they are taxonomic, they constitute the initial step toward understanding the organisms of the Gulf and of the Mediterranean. The natural second step must be ecological, i.e., determination of how the various species are related to their environmental complexes. Then would follow the more intensive studies of structure, function, and behavior required to understand how and why the organisms maintain these relations. Little more than the first step has been taken, for, according to Kofoid (1910, p. 20), "the Station has not as yet undertaken any systematic exploration of pelagic, abyssal, or littoral fauna, though much of the work of collection, the records of seasonal occurrence, and the individual researches thus far published afford a basis for the beginning of such enterprises." But, however limited the actual achievements may be, the Station is engaged in a programme of research having for its object complete understanding of the structure, function, and behavior of the organisms by virtue of which they are adapted to the marine environments of the Gulf of Naples and the Mediterranean Sea. When this type of investigation shall have been carried beyond the preliminary taxonomic stage, the Naples Station will be engaged *strictly* in researches in marine biology.

The two types of investigation, general biology and marine biology, are intimately related to each other. The same organisms may be dealt with and largely the same methods of study may be employed, but the point of view which gives direction to each piece of research is fundamentally different. In the former type, marine organisms are regarded as tools to be used in solving some morphological or other problem relative to land and fresh-water organisms as well. In the latter type, morphological and other methods are employed for the purpose of understanding marine organisms. Both types of investigation are indispensable. Who could justly maintain one to be necessarily more productive to biology than the other? If the purpose of biology is to fully understand organisms, it follows that general biological researches must contribute toward this end, but it also follows that investigations having for their object complete understanding of marine organisms,

fresh-water organisms, or land organisms—as such—must, by very definition, contribute toward the same end. Yet, while the value of the former type of investigation is widely appreciated, that of the latter is not.

With few noteworthy exceptions, among the foremost of which stands the Port Erin Marine Biological Station, it is not the marine biological stations but enterprises such as the Monaco Institute of Oceanography, the great oceanographic expeditions, the fisheries laboratories like the United States Fisheries Stations at Woods Hole, Massachusetts, and at Beaufort, North Carolina, and the International Commission for the Investigation of the Sea, that have contributed most to the science of marine biology. The great majority of marine biological stations are devoted to general rather than marine biology and, of course, collect their material when, where, and how it may be best obtained without regard to the problems of marine biology. They rarely trouble themselves with questions concerning the seasonal, vertical, horizontal, or topographical distribution of any species of marine plant or animal. They frankly make no attempt to determine how or why variations in the distribution of organisms are correlated with fluctuations in light, temperature, salinity, gas-content, and other elements of their environments, or of how any species is ecologically related to any other species.

It has been contended that such matters pertain only to ecology; that they involve no problems in morphology, embryology, cytology, or physiology. Is ecology, then, the major part of marine biology? Are morphology, embryology, and physiology secondary in importance? Obviously not, for no act of any organism can be fully described in terms of behavior alone, function alone, or structure alone, or even in terms of the organism alone. Every vital act is virtually a moving equation between the organism, a highly integrated system of structures and functions, and the environmental complex. *The way in which organisms are distributed with respect to each element of this environmental complex, and how they behave so as to maintain this distribution is all ecology, strictly speaking, can tell us.* Why they are so distributed and why they behave as they do are fundamentally morphological and physiological problems; problems difficult to solve, perhaps, but none the less real and significant. It must not be forgotten that every act involves an actor; that distribution and behavior imply some morpho-physiological thing which is distributed and which does the behaving. Does it not follow that a peculiar or unique distribution and behavior presupposes an equally peculiar or unique

organism which is describable only in terms of structure and function? To make this description is fully as important and essential for understanding the relations maintained between organisms and their environments as anything an ecologist—as such—can reveal.

Why is the copepod *Calanus finmarchicus* typically more abundant in the San Diego region than its near relative *Eucalanus elongatus?* Why is *Sagitta enflata* captured in the San Diego region only within ten fathoms of the surface, while *S. lyra* is seldom captured above one hundred fathoms? Why does the ctenophore *Pleurobrachia bachei* increase in abundance on the surface as the temperature of the water increases from 16° C to 20° C, and why have specimens exceeding nine millimeters in height never been taken from water exceeding 17° C, although they occur abundantly in colder water? As the temperature of the water increases between 15° C and 20° C, why are the zoöids of the sexual generation of *Salpa democratica* obtained from the surface in decreasing numbers while those of the asexual generation are obtained in increasing numbers? Such problems are as fundamentally morphological and physiological as they are ecological, but most marine biological institutions almost completely ignore them. They are admittedly outside their chosen lines of research. Yet no marine organism can be well understood until many problems such as these are solved.

What of it? What value has the fact that four hundred individuals of a particular species were obtained when the temperature of the water was 20° C, while only one hundred were obtained when it was 15° C? May it not have been a mere coincidence due to the effect of random sampling? Why, then, waste time tabulating data when they apparently concern facts of no importance in the life of the species involved?

These questions carry the subtle implication that the value of facts can be predicted in advance of their observation; that, unless the bearing of certain classes of facts upon some dominant theory can be foreseen, it is foolish to study them. Theories of evolution, heredity, variation, adaptation, and selection must, of course, be formulated before they can be proved or disproved. But nothing is more certain than that they ought to be formulated in consequence of as well as in preparation for investigations. Otherwise induction would be replaced by deduction and then no observation would be worth while unless the facts which it revealed were first deduced from theory.

But this *modus operandi* is not science. A little reflection will convince anyone that science affords no means exclusive of observation of deciding whether particular facts of nature are or are not worth observing. Searching investigation alone is capable of determining what value attaches to the fact that four hundred individuals of a particular species were obtained when the temperature was 20° C and only one hundred when it was 15° C. If it actually turns out to be a coincidence due to random sampling, investigation alone can demonstrate it. If it is important to the life of the species involved, investigation alone can demonstrate that. Is it not unscientific to pronounce any facts of nature valueless prior to their investigation? Is not the examination of facts irrespective of their bearing on any dominant theory a necessary step in any strictly scientific programme of research?

Still, if this be granted, it is evident that no one man or institution could hope to study every aspect of marine biology any more than he could of general biology. Practically, it is necessary to select small groups of problems. What, then, is the likelihood that detailed hydrographic investigations will yield profitable biological returns?

Superficially, it looks as if undue emphasis were being placed upon the environment; as if hydrography were masquerading under the name of biology. Such, indeed, is too frequently the case in many so-called ecological researches, and it is certain to be the case unless the hydrographic observations are made subordinate to the biological ones. When this caution is observed, however, hydrography becomes as indispensable as any recognized branch of biology itself for understanding marine organisms; for, obviously, a marine organism is an organism that is primarily marine. It can live only within certain limits of temperature, salinity, density, and so on, of the water. To imply, therefore, that it is a waste of time to define these limits for each species, and to determine to what particular temperatures, salinities, and densities each species is best adapted, amounts to contradicting the fact that marine organisms live. Surely, to learn how they live and what they do is as fundamental, biologically, as to learn how they are reproduced and of what they are constructed. It follows, then, that when properly subordinated to biology, hydrographic investigations yield as important biological returns as do investigations that in themselves are biological.

Therein lies the value of realizing that the true goal of marine biology is the acquisition of full and complete knowledge of every

phenomenon touching the life of every animal and every plant in the sea. Adherence to this ideal, though unattainable in a literal sense, has a sobering effect upon investigation, and gives it a definiteness and co-ordination which it may otherwise lack. The particular problems selected for investigation will then be determined entirely from the point of view of feasibility and not from that of how they may prove or disprove a dominant theory. What particular group of problems would it be most practicable to investigate at this particular time, in this particular region, and in regard to available resources and information already at hand?

The Scripps Institution looks at the matter in this way and, although not restricting itself to marine biology, its efforts have been largely spent toward gaining an understanding of the relations maintained between organisms and their natural environments. No other aspects of biology seem of greater importance at the present time, and the Institution is so situated as to make this study peculiarly practicable. But, as Ritter (1915, p. 232) says:

> The managing board have no delusions as to the uniquely "burning" character of the questions under investigation, or as to its having reached the threshold of the Ultimate Mystery of Life and Death. Its profound belief in the importance of biologic truth to the welfare of human kind is of such sort that it knows that many other problems being studied by many other men and other institutions are no less vital than those engaging its efforts; and that problems of tomorrow, next year, next decade, next century, while different from those of today, will be no less numerous and no less insistent than those of today. It holds every item of positive knowledge of the living world essential to the scientific interpretation of that world; that such interpretation alone can beget a right attitude toward that world; and that the high level of man's development which we call civilization is wholly dependent upon a right attitude on the part of the largest number possible of the community toward all things that live.

3. Field Observation vs. Laboratory Experiment

Some time ago Whitman (1902, p. 504) made this statement:

> The fundamental problems of heredity, variation, adaptation, and evolution cannot be wholly settled in the laboratory. They concern vital processes known only in living organisms—processes which are slow and cumulative in effects, expressing themselves in development, growth, life-histories, species, habits, instincts, intelligence. These problems require, therefore, to be taken to the field, the pond, the sea, the island, where the forms selected for study can be kept under natural conditions, and where the work can be continued from year to year without interruption.

Though true, says the experimentalist partisan, this is an obviously impracticable ideal; and while such problems cannot, perhaps, be "wholly settled in the laboratory," their really essential features can be satisfactorily worked out by the experimental method. Laboratory experiments have demonstrated the physiological mechanism of response involved in many reflex actions, instincts, and habits, and have greatly clarified our vision as to the probable origin of memory, reason, and other complex functions of consciousness. Indeed, the literature of animal behavior abounds in such terms as phototaxis, geotaxis, thermotaxis, and chemotaxis, all of which pay tribute to the ingenious achievements of laboratory experiments. Do not the results justify the claim that all really essential knowledge concerning the relation between marine organisms and their environments can be more accurately and much more expeditiously ascertained by subjecting a few typical organisms to laboratory experiments than by investigations prosecuted in the ocean itself? Does not the laboratory method eliminate the expense and time-consuming task of analyzing hydrographically hundreds upon hundreds of water-samples?

Experiments conducted in a laboratory are and always will be indispensable but, after all has been said, *they reveal only what transpires in a laboratory and are necessarily incapable of revealing what occurs in nature.* Whitman's ideal, though impossible of complete realization, could and would come much nearer realization than is at present the case were the indisputable fact more widely appreciated that no method of laboratory experimentation can reveal the natural behavior of an organism unless it is possible to re-create nature in miniature. Even if certain environmental conditions can be reproduced in a laboratory, the total complex cannot be duplicated. Certain stimuli occur in nature which are necessarily absent in the laboratory, and others are probably introduced in the laboratory which do not occur in nature. This is particularly true with respect to the ocean. How, for instance, could the stimuli associated with depth, distance from the coast, velocity of current, or wave action be duplicated? Moreover, the nature of an animal's response depends upon the duration as well as upon the intensity of any particular stimulus, and upon other preceeding and attendant stimuli. This fact makes it obvious that laboratory experiments can offer no reliable evidence concerning an animal's behavior in nature. Says Yerkes (1914, p. 181):

> It would appear to be self-evident, yet the attitude of many experimental students of animal behavior seem to contradict the statement, that every

student of animal life should be familiar with the objects of his interest in nature as well as in the laboratory: that he should possess, as a basis for evaluating the results of experiments, intimate knowledge of the instincts, habits, temperaments, and habitat of whatever type of organism he happens to be using for experimental purposes.

Even if the natural environment could be duplicated, another insuperable difficulty confronts the laboratory experimentalist. He is compelled to restrict his experiments to a few individuals; but he always applies his conclusions to races, varieties, species, or some other similar group of organisms. How can he be sure that the behavior of the individuals selected is typical of that of the group as a whole? He cannot, no matter how large the number of individuals experimented upon, unless he knows in considerable detail the environmental conditions at the time and place his selected individuals were collected; and unless he knows how the group as a whole is distributed with respect to variations in the environmental element he deals with in his experiments. An illustration will make this clear.

The species of chaetognatha most characteristic of the San Diego region, *Sagitta bipunctata,* increases in abundance on the surface from noon until some time after sunset, when it attains a maximum; but large numbers may occur on the surface at all times of day and night —even at noon. Is it reasonable to assume that individuals collected at noon would react in the same way to variations in light intensity as those collected after sundown? Yet the latter are most typical of the species as a whole. Again, the species decreases in abundance on the surface as the temperature increases above 15° C, but large numbers are normally present at all temperatures. Is it reasonable to assume that those collected on the surface when the temperature was 20° C would react to variations in temperature like those collected when the temperature was 15° C? Yet the latter are most typical of the species as a whole. Similar phenomena occur with respect to variations in salinity, and probably with respect to variations in gas-content, and other environmental elements.

Obviously, the magnitudes of each element of an environmental complex may act like so many sieves separating the individuals of any one species into a variety of behavior-classes. Reactions witnessed in a laboratory, therefore, may be largely due to the particular individuals collected. If this is so, intensive investigation of the organism in its natural environment is a necessary preliminary to generalizations from laboratory experiments on behavior: if it is not so, that fact must be proved in each particular case, or conclusions applied to the species (or

other taxonomic group) will be founded upon an unjustified assumption. In either case, the facts to which this assumption relates must be investigated; they cannot be argued out of existence or into existence. Science, if really scientific, must ever proceed by induction: it must observe, describe, and classify all ascertainable facts before it can justify any generalization involving those facts. For deduction unsupported by induction, "carries the implication that great numbers of facts of nature can be explained without having been themselves examined." (Ritter and Johnson, 1911, p. 432.)

The substitution of pseudo-scientific speculation for rigorous inductive method reaches its extreme, perhaps, in Ostwald's (1902) viscosity theory of vertical migration. Basing his speculations on a literal interpretation of the commonly accepted definition of plankton as "die Summe der *schwebenden* [italics mine] Wasserorganismen," which he (p. 596) holds to be "die allgemeinste und entsprechend gröbste Definition des Planktons," Ostwald develops his theory: "nicht durch Zussammenfassung von Einzelthatsachen," but "aus physikalish-chemischen Voraussetzungen und einigen sehr allegmeinen Lebenseigenschaften des Planktons." He reaches the conclusion that variations in viscosity of the water, induced mainly by diurnal and other periodic variations in temperature, cause plankton organisms to rise and fall, thus accounting for vertical migrations.

The theory is ingenious and, like many similar ones, is provided with innumerable "cubby-holes" in which the main purport of the theory may be conveniently concealed. It would consume more space than this paper permits to point out all its fundamental weaknesses. This much, however, must be said: the assumption upon which the theory rests is absurd, if literally interpreted, for organisms are not corks, and the most characteristic quality of an organism consists in its ability to live—not in its ability to float or remain in suspension. This tendency, so frequently displayed by biologists, to eliminate the organism from consideration and substitute physical and chemical processes for its activities, could not be scientifically justified even if that organism had been manufactured of physical mixtures and chemical compounds. It is precisely such substitutions that characterize Otswald's theory.

Even if variations in viscosity were the main causes of vertical migration, observation demonstrates specificity in their effects: *Sagitta bipunctata* occurs on the surface in larger numbers between 6 and 8 A.M. than at any other time between midnight and noon; *Calanus*

finmarchicus does not. Why? Obviously, no physico-chemical theory like Ostwald's can explain such facts unless, as is not infrequently the case, one selects only the facts which fit and ignores those which do not fit. "Every truly vital chemico-physical problem of organisms," says Ritter (1915, p. 231), "is two-phased: how do the chemico-physical attributes of the constituent substances act upon and so explain the organisms; and what particular structures and activities are the chemical substances caused to manifest by being constituents of and used by the particular organisms?" Specificities in the vertical migrations of *S. bipunctata* and *C. finmarchicus* can be physico-chemically accounted for only by corresponding specificities in the physico-chemical makeup of the organisms. The main value of Ostwald's theory consists in pointing out that variations in viscosity are involved in the phenomena of vertical migration. It, of course, contributes something to the explanation of these phenomena, but very little.

Laboratory experiment and field observation must go hand in hand. The former cannot, except by inference, ascertain the manner in which a species is related to its environmental complex. The latter cannot, except by inference, ascertain the nature of response involved in correlations observed between marine organisms (or any other kind of organisms) and their environments. Observation alone cannot determine whether the observed correlations are due to tropisms, trials and errors, or some indirect metabolic reactions. Experiment alone cannot reveal the fact that *Sagitta bipunctata,* for example, is usually more abundant between fifteen and thirty fathoms than at any other depth; that it decreases in abundance below this depth much more slowly than it does above it; that it maintains its maximum abundance at higher levels during the summer (July to October) than during the winter (November to March); that it decreases in abundance as the distance from the coast increases at all depths above twenty fathoms, while it increases in abundance at all depths below thirty fathoms, etc. These facts pertain to the species' behavior and have played their rôles in its evolution just as certainly and to fully as great an extent as is the case with any facts of behavior demonstrated in a laboratory. Assuredly, both sorts of investigation are required in order to approach, even remotely, complete knowledge of the behavior of any species. "That old and true method of natural history," says Whitman (1902, p. 505), "—*observation*—must ever have a large share in the study of living things. Observation, experiment, and reflection are three in one.

Together they are omnipotent; disjointed, they become impotent fetishes. The biology of today . . . has not too much laboratory, but too little of living nature."

4. Complexity of Hydrobiological Relations

On June 17, 1909, four surface hauls (p. 160, hauls 1659–1662) were made off La Jolla with the same net while the "Agassiz" was tied to its mooring. The temperature of the water was 18°4 C during all four hauls. Yet, the first haul (5:00 to 6:00 P.M.) caught thirteen specimens of *Sagitta bipunctata*, the second (6:00 to 6:45 P.M.) caught none, the third (6:45 to 7:30 P.M.) caught 550, and the fourth (7:30 to 8:00 P.M.) caught none. Thus, the number of specimens varied erratically from none to 550, and the third haul caught about fifty-six times more per hour than the first, an increase of fifty-six hundred per cent in one hour and a half. It is evident, from the constancy in temperature, that the current, and hence the volume of water filtered, could not have varied to an extent corresponding, even roughly, to the difference in number of specimens obtained. Moreover, it is unlikely that any progressive hydrographic change associated with such a brief time interval could have caused first a decrease, then an increase, and finally another decrease in number of specimens obtained.

Someone may see in this example a demonstration that hydrographic investigations can yield little definite information concerning the relation of this species to the conditions of its environment. Does not the instance prove this species to be erratically distributed with respect to temperature and other hydrographic conditions; that the condition of the environment had nothing to do with the variability noted? On the face of the matter it seems so. Yet it is fairly well established that *Sagitta bipunctata* is definitely affected by fluctuations in the temperature of the water. On the surface it decreases in abundance, on the average, as the temperature increases above 16° C. Furthermore, every depth thus far investigated (5, 10, 15, 30, 40 and 50 fathoms) shows that the species increases in abundance as the temperature increases from 9° C to 14° C, and decreases as the temperature increases from 16° C to 21° C. In other words, the species maintains a maximum abundance when the temperature lies somewhere between 14° C and 16° C, in spite of the fact that the above instance gives no indication of it. The fact that one case apparently

contradicts this generalization really signifies that the natural variability in plankton distribution is so large that the hydro-biological relations will be masked unless large numbers of searching and fairly continuous hydrographic observations are made which correspond in time and place to net hauls. Says Herdman (1908, p. 56):

> It is clear that samples taken quarterly, monthly, or even fortnightly, are quite inadequate to convey a correct idea of the constitution and changes of the plankton of a sea-area in any detail; and, consequently, conclusions ought not to be drawn from such insufficient observations. Samples taken weekly throughout the year, and almost daily during the . . . most critical months, give by no means too much information, but will probably suffice to enable one to make that detailed comparison between adjacent localities and dates which are necessary for the purpose of determining the representative value of such periodic samples.

The complexity of hydrobiological problems is well illustrated by Herdman (1907, p. 37). On April 1, 1907, one mile north of Port Erin, Isle of Man, two "exactly similar" surface nets were towed side by side for fifteen minutes. One net (which we shall designate as A) was hauled in, emptied, and put out again at the expiration of the first eight minutes, while the other net (B) was not touched. The first half of the haul with A did not contain a single crab zoëa, but the last half contained essentially the same number as the uninterrupted haul with B did. In both there was "an extraordinary number of crab zoëas, rendering the ends of the nets quite dark in color." This is "incontrovertible evidence of the sharply defined nature of a shoal of organisms . . . [and forms] . . . an instructive example of how nets hauled under similar circumstances a short distance apart may give very different results."

In spite of the many similar instances that might be cited, there seems to be a widespread impression that one, or at most a very few hauls with a net of known filtering capacity justify conclusions concerning the number of each species present over large areas of the sea. It is not fully appreciated that the number and kind of organisms caught by any one net haul at any one depth, time, and place is consequent not only upon the volume of water filtered, but upon the temperature, salinity, gas-content, and chemical composition of the water; upon the effects of wind, clouds, fog, rain, snow, ice, light, and season; and upon many strictly biological influences, such as stage of growth, period of reproduction, food relations, and periodic activities. Though collecting apparatus be as perfect as human ingenuity can devise and the volume of water filtered be known to the smallest

fraction of a cubic millimeter, neither can obviate the necessity of making large numbers of hauls in restricted areas, and tabulating the hydrographic conditions corresponding to each.

The objection may be made that the examples cited above were cases of extreme, not typical, variability. Let us then consider certain typical instances relative to the San Diego region. When the specimens of *Sagitta bipunctata* obtained in each of twenty-five surface hauls made with a 000 net between 4 and 6 A.M. during June and July, 1908–09, are counted, the mean abundance is found to be 260 per hour, while the *mean variability*[2] is 345. Between 6 and 8 A.M. twenty-one hauls give a mean abundance of 317 and a mean variability of 448; between 8 and 10 A.M. twelve hauls give a mean abundance of 230 and a mean variability of 357; between 10 and 12 A.M. thirteen hauls give a mean abundance of 10 and a mean variability of 14; between 12 and 2 P.M. thirteen hauls give a mean abundance of 16 and a mean variability of 21; between 2 and 4 P.M. thirteen hauls give a mean abundance of 15 and a mean variability of 18; and between 4 and 6 P.M. twelve hauls give a mean abundance of 34 and a mean variability of 45. The list might be continued indefinitely, and similar data might be presented relative to copepods, schizopods, ctenophores, salps, etc. All reveal a mean variability which *nearly always exceeds the mean abundance.* Thus, in the above instance, it is 1.3 times the abundance between 4 and 6 A.M.; 1.4 between 6 and 8 A.M.; 1.5 between 8 and 10 A.M.; 1.4 between 10 and 12 A.M.; 1.3 between 12 and 2 P.M.; 1.2 between 2 and 4 P.M.; and 1.3 between 4 and 6 P.M.

The significance of these facts is obvious. The accidental error involved in a single net haul due to the natural variability in plankton distribution exceeds, on the average, the true mean abundance which the single haul attempts to measure. In other words, *if the volume of water filtered can be estimated within an error of one hundred per cent nothing can, as a rule, be gained by more accurate measurement.* Stated again, if the "filtration constant" is approximately known, and if the mean velocity of current can be estimated, say as 6 ± 6 kilometers per hour, the mean number of plankton organisms present per cubic meter of water throughout the San Diego region can be determined *just as accurately as if the "filtration constant" and velocity of current were known with the most extreme accuracy conceivable.*

[2] By mean variability is meant the average of all differences between the mean abundance and the abundance indicated by each haul. It is not equivalent to the standard deviation.

More time spent in repeating hydrobiological observations under the same controllable conditions, rather than in computing "filtration constants" and improving the accuracy of the apparatus, is the most urgent need. Not only is time wasted in needless refinement of apparatus, but, as Thorndike (1904, p. 158), says:

> Much ignorance is shown by the many students who disparage all measurements that are subject to a large variable error. They either do not know or forget that the reliability of a measure is due to the number of cases as well as to their variability, and that in the more complex and subtle . . . [phenomena] . . . it is always practicable to increase the number of measurements, but often impossible to make them less subject to variable errors. They also forget that the natural and real variability of the fact itself is often so large as to make the variability due to errors of instruments and observation practically negligible.

Once this fact is grasped it will be evident that the methods of collecting and exploring employed by most oceanographic expeditions, like the "Challenger," "Blake," "Valdivia," "Siboga," and even the German plankton expeditions, cannot reveal in any detail the relations maintained between plankton species and their environment. The methods are adequate only for determining the kinds and range of species over extensive areas and for yielding general descriptions of the associated environments. The results embodied in the numerous excellent monographs and reports, while detailed and comprehensive taxonomically, afford little, if any, reliable evidence concerning the relative abundance of the various species in their horizontal, vertical, or seasonal distribution. The methods are adequate for purposes of scientific reconnaissance, but are not adapted to yielding that detailed hydrobiological information without which the first step toward understanding the habits of any marine organism is impossible. It is evident that no institution can obtain this required information unless its efforts are primarily biological rather than oceanographical.

5. Quantitative Methods Employed at the Scripps Institutions

There are several marine institutions in Europe that recognize the necessity of quantitative investigations. Among the foremost may be mentioned the Commission for the Scientific Investigation of the German Seas, the International Commission for the Investigation of the Sea, and the Marine Biological Station at Port Erin, Isle of Man. To these we are indebted for much mathematical and experimental knowledge concerned in quantitative estimates of marine organisms, as well as for apparatus for collecting them and for analyzing the

physical and chemical conditions of the sea. The two commissions, however, especially the German one, have based nearly all their researches upon an assumption of uniformity in the distribution of the smaller organisms over large areas, and the Port Erin Station is to be credited especially with having demonstrated, very completely, the serious error involved in this assumption. Furthermore the two commissions differ radically from the Port Erin Station, in that the latter is engaged in intensive rather than extensive investigations, and recognizes the necessity of frequently repeated hydro-biological observations in very restricted localities.

The Scripps Institution has followed, in general, the lead of the Port Erin Station, but differs, perhaps most conspicuously, from all three European institutions, in that its primary interest is in pure rather than economic biology. Its methods are based on the conviction that large numbers of somewhat crude hydro-biological observations, rather than precision of apparatus and exact computations of "filtration constants," will reveal the relations maintained between organisms and their environments. After such observations are made the data are subjected to rigorous examination. Two methods of treating the field data are used; the frequency method and the abundance method.

The frequency method consists in arranging all the biological hauls in order of the magnitude of one of the environmental elements, say temperature; separating them into groups so that the temperature range in each is the same, say two degrees; and noting the hauls in any one group containing the particular species under investigation. Then, by expressing the number of these hauls as a percentage of the total number in that group, a measure of the frequency of occurrence of the species within the limits of that temperature interval is obtained. Proceeding similarly with all the other groups, the relative frequency of the species under the different temperature conditions is found. By this means variations in the frequency of the species may be quantitatively compared with fluctuations in the elements of its environmental complex, correlations between the two established, the reliability of the correlations tested by statistical methods, and conclusions of significance drawn.

The abundance method is similar in every way to the frequency method except that, instead of depending upon the mere presence and absence of the species, the specimens in each haul are counted. Consequently, the average number of specimens per unit volume of

water filtered during each haul may be computed and compared with each other. This, of course, is much more accurate and makes a more thoroughgoing statistical treatment possible.

Preliminary and supplementary to the employment of these quantitative methods, the data are examined in a more cursory manner for the purpose of ascertaining, in a general way, the degree of correspondence between the biological and hydrographic data. For example, the center of population of *Sagitta bipunctata* undergoes a seasonal oscillation from its maximum depth in winter to its minimum depth in summer. In attempting to find a corresponding oscillation in one of the environmental elements, the temperature range pertaining to this center of population was discovered to be confined to a larger and deeper depth interval in winter than in summer. Combining these two facts a single descriptive statement is obtained, namely, that the vertical oscillation of the center of population is apparently correlated with a corresponding oscillation of the temperature distribution, or "thermocline." In order to test the extent and validity of this apparent correlation recourse is had to the more rigorous methods just described.

A more detailed consideration of these methods would require more space than is available in this paper. It would involve discussing the relation between frequency and abundance, how the frequency may be standardized when the average volume of water filtered differs, and how the unit volume of water filtered is measured. It would necessitate considering the use of geometric means, coefficients of association, coefficients of preference, methods of eliminating the effects of one variable upon the others, and methods of dealing with accidental and systematic errors. It would require an explanation of why the usual methods of linear and multiple correlation, and the probable error method cannot be legitimately applied to distribution problems of the type herein considered; and it would require an explanation of the methods employed in their places. Suffice it to say, therefore, that other papers are being prepared in which all of these matters will be discussed in detail. It is hoped, however, that this brief account will give some idea of the methods employed.

6. Summary and Conclusion

In the foregoing discussion it has been shown that:

1. The function and, strictly speaking, the only function of marine biology is to understand marine organisms.

2. Broadly interpreted, this means that the significance of no phenomenon essential to the life of any marine organism can be fully understood so long as any other phenomenon likewise essential to it is entirely ignored.

3. The majority of marine biological institutions are not engaged in marine biology, but are supporting researches in general biology which only incidentally contribute to marine biology.

4. Hydrography is as indispensable as morphology, embryology, cytology, or physiology for understanding the marine organism.

5. No method of laboratory experimentation can discover an organism's behavior in nature.

6. Hydrobiological relations are too complex to be determined without searching and fairly continuous observations made in a restricted region.

7. The natural variability in the distribution of marine organisms is so great as to make errors of collecting apparatus practically negligible.

8. Only an institution primarily engaged in marine biology rather than oceanography or economic biology is in position to investigate comprehensively the hydrobiological relations of marine organisms.

It is hoped this introduction will help to make the hydrographic data and Dr. McEwen's "Summary" contained in this volume appear as interesting and indispensable to the marine biologist as to the hydrographer of this coastal region.

Transmitted March 30, 1916.

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